ON THE LEAF-ANATOMY OF *SCÆVOLA CRASSIFOLIA*, WITH SPECIAL REFERENCE TO THE EPIDERMAL SECRETION.

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(Plates xxvii.-xxviii., and six Text-figures.)

Introduction.

Scævola crassifolia forms a prominent element in the sand-dune flora near Adelaide, where it occurs in association with *Spinifex hirsutus*, with such shrubs as *Olearia axillaris*, *Leucopogon Richei*, etc., and with smaller plants such as *Pelargonium australe*, *Lotus australis*, *Œnothera biennis* (introduced), and *Senecio lautus* (**3**, p.584).

In habit, *S. crassifolia* is a low, spreading shrub, which is able, by lateral growth, to occupy large areas of the dune. Its older woody stems form a dense undergrowth, in which a quantity of blown sand and dried leaves of Posidonia are accumulated, thus helping to build up the dunes. *S. crassifolia* is able to survive burial in sand by an upward elongation of the stem, and by the development of adventitious roots.

Owing to the extreme stickiness of the buds and young leaves, the varnishing or lacquering of the surface of older leaves, the dullness of surface, and the succulence of mature leaves, it was thought that an examination of the leaf-anatomy would prove interesting. The investigation was carried out in the Botanical Laboratory of the University of Adelaide, at the suggestion of Professor Osborn, to whom I am much indebted for his constant help and encouragement.

Summary of Previous Investigations.

Despite its particular interest, the N.O. Goodeniaceæ has received but scant attention at the hands of botanists. As early as 1876, Vesque(**5**) published an account of the anatomy of *Goodenia ovata*, which, however, was restricted to an investigation of the anomalous stem-structure. With this, he compared the stems of *Scævola crassifolia*, *S. Plumieri*, *S. microcarpa*, and *S. spinescens*, but there is no investigation of leaf-anatomy in any of these species.

In the Systematic Anatomy of the Dicotyledons (i., p.471), Solereder gives a brief account of the leaf-structure of the Goodeniaceæ, based upon his own observations of *Goodenia ovata*, *Selliera radicans*, *Scævola Plumieri*, and *Dampiera Brownii*, and upon those of Briquet in the case of *Brunonia*. He records that the stomata may occur upon both surfaces, or upon the lower surface only, and that the number of subsidiary cells, when these are present, is four, two of which are placed parallel to the pore, the other two being applied to the narrow ends of the guard-cells. In form, the leaf is found to be typically bifacial, as exemplified by *Dampiera Brownii*, but is sometimes centric, as in *Scævola Plumieri*. Silicified groups of cells are common, in the formation of which certain epidermal and the adjacent mesophyll-cells take part. As well as the ordinary clothing-hairs, which are characteristic of most members of the Order, peltate, glandular hairs have been observed in *Goodenia ovata* and *Scævola Plumieri*. These are described as being "shortly stalked, peltate glands, the shield of which consists of a few cells separated by radial walls."

The above account is a summary of our present knowledge of leaf-anatomy in the Goodeniaceæ. It is interesting to note that, in none of the plants hitherto investigated, has any copious, epidermal secretion been described. In *S. crassifolia*, however, the buds and young leaves are coated on both surfaces with a thick layer of sticky resin, which is secreted by numerous, stalked, glandular hairs.

The secretion of mucilage or resin, or both together, has long been recognised as a method of bud-protection. Groom(**2**) has given an interesting account of the mucilage- and resin-secreting organs of buds. This work is restricted to those plants which bear "colleters" or "villi" on the stipules. These "colleters," which are almost invariably pear-shaped, multicellular bodies, in which a peripheral palisade-layer secretes the mucilage or resin, are only functional in the bud, and fall off with the stipules. Only in one case—that of *Wormia Burbidgei* (Dilleniaceæ)— does Groom record an instance of the secretion being derived from glandular hairs on the leaves themselves, but, of this, no description is given. Volkens(6), however, has described many plants in which the secretion is not only derived from glandular hairs on the leaves themselves, but is also produced for a long period of time, sometimes till maturity of the leaf. It is to Volkens that we owe what knowledge we have of "leaf-lacquering" as a xerophytic adaptation.

In the present investigation, the development of the leaf is traced from the earliest stages to the mature condition, with special reference to the glandular covering in the juvenile state, the function, and fate of its secretion.

Morphology of the Shoot.

A shoot of *Scævola crassifolia* is characterised by the vertical arrangement of the leaves, which is consistent from the leaves in the bud to those farthest away from the growing apex. The leaves are all ovate, more or less toothed, petiolate, the base being closely applied to the stem on its upper side. The leaf-teeth are more marked in the bud and young leaves than in the mature leaves, in which they are often obliterated by secondary increase in thickness. The terminal bud is small, and, during the growing season (August to October, the Spring months about Adelaide) it is hidden by the rapidly expanding young leaves. Later, when this activity ceases, the bud is hidden at the base of the most distal leaf. The leaves in the bud are not folded about one another; they are opposite and vertical, the morphological upper surface of one leaf being closely glued to the upper surface of the next youngest leaf.

The whole growing region of the shoot in *S. crassifolia* is covered with a sticky secretion, which gradually dries up farther away from the stem-apex. As the leaves become expanded from the bud, they increase rapidly in surface-area, and later lose their extreme stickiness. They are, at this stage, characterised by glistening patches of drying secretion, which give them their varnished or lacquered appearance.

The mature leaves are large, thick, and succulent, and present a dull surface. Despite the fact that the secretion tends to dry up on the expanded portion of the older leaves, the leaf-base is always distinctly sticky, even in the mature leaves. In this manner, the axillary buds are covered by secretion.

The young flower-buds are borne in dense, terminal spikes. As is usual in the Goodeniaceæ, the calyx is inconspicuous, and the corolla protects the essential parts of the flower. In *S. crassifolia*, each flower is situated between two bracteoles, and is subtended by a bract, which is glued to the exposed surface of the bud by means of its sticky secretion. The glandular hairs, from which the secretion is derived, are of the same nature as those on the leaves.

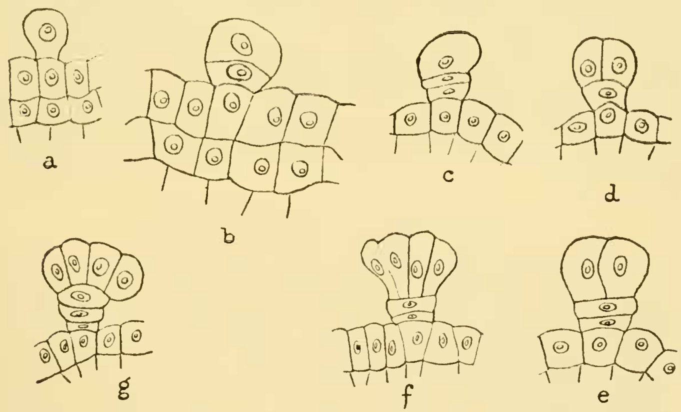
Distribution of the Actively Secreting Glands.

It is in the buds that the glandular hairs reach their maximum development. Upon examination of a section through the apex of a shoot, it will be seen that the rudimentary leaves, even before they are completely differentiated from the stem-apex, are provided with numerous, closely-set, mature, actively secreting, glandular hairs. These hairs are more abundantly developed on those surfaces which are exposed earliest. In the bud, there is a continuous production of glandular hairs, the various stages in development being found mingled with the mature glands. These developmental stages are not restricted to the youngest portions of the bud, nor to any particular part of the leaf, but, as will be seen later, apparently any epidermal cell up to a certain stage in development, may form a gland (Pl. xxvii., fig.1). In this manner, new glands are provided to keep pace with the increase in surface of the leaf, the secretion of which will prevent the sticky coat from being broken at any point.

Once the young leaves are freed from the bud, glandular hairs are no longer formed; upon such leaves only, the mature condition is found. The distance between these glands tends to increase as the leaf-surface increases in area by the differentiation of the leaf-tissues. In the older leaves, the glands lose their activity, except as mentioned above, in that region where the leaf-base clasps the stem. There, the glands remain active throughout the life of the leaf. A section through this region shows an abundant development of glandular hairs of the same nature as those on the young leaves. By the activity of these glands, the axils of the leaves are filled with secretion, and provision is made for the protection of the axillary buds. At the junction of the stem and leaf-base is a circlet of long, multicellular clothing-hairs (Pl. xxvii., fig 2). These were tested for resin and mucilage, with negative result.

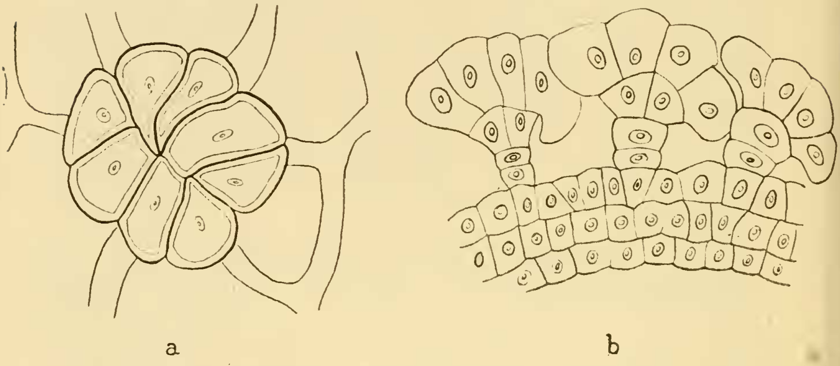
The Development of the Glands.

That the glands are hairs, is evinced in the manner of their origin from a single epidermal cell. Any epidermal cell may form a gland. The cell enlarges, the nucleus divides, and a horizontal wall is formed separating two cells, the uppermost of which becomes considerably enlarged and spherical in outline (Text-fig. 1, *a*). A second, horizontal wall cuts off the rudiment



Text-fig. 1.—Stages (*a*-*g*) in the development of the glandular hairs; (× 530).

of the stalk at the base of the spherical cell, which latter is destined to become the head-cell of the gland (Text-fig. 1, *b*). At this stage, either a second stalk-cell is formed (Text-fig. 1, *c*), followed by a median, vertical division in the head-cell (Text-fig. 1, *c*), or the latter division takes place before the formation of the second stalk-cell (Text-fig. 1, *d*). A third stalk-cell is now formed, either preceded or followed by the ultimate divisions in the head-cells (Text-fig. 1, *f*, *g*).



Text-fig. 2: *a*, surface-view of a mature gland; *b*, part of section through young leaf, to show crowding of mature glands, and overlapping of shields; (× 530).

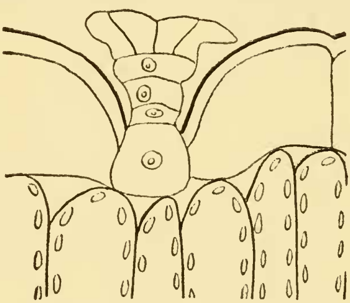
The head of the mature gland forms a shield of eight cells, only four of which are seen in transverse section (Text-fig. 2, *a*). The shield, which is ultimately reflexed at the sides, is borne upon a stalk of three tiers of cells, the two lower tiers being composed each of a single cell, while the upper is composed of two cells, which grow out laterally to support the head-cells (Text-fig. 2, *b*).

The Nature of the Secretion.

The secretion, which covers both upper and lower surfaces of the leaf, is a yellowish, translucent, homogeneous substance, which is soluble in alcohol. It is very sticky when fresh, and gives the characteristic red colouration of resin when tested with Alkanna root-extract. A test for mucilage, carried out with corallin-soda, gives a negative result. The secretion reaches its maximum thickness in the bud, every available space between the young leaves being filled up. This fact, which is probably a result of the continuous production of glands in the bud, indicates that the secretion of resin in *S. crassifolia* is primarily concerned with bud-protection.

The secretion is still mobile upon the young leaves outside the bud, but since no new glands are being formed to keep pace with the increase of leaf-surface, it becomes spread out over a greater area and, consequently, more attenuated. The thickness of the film of secretion varies in different parts of the same leaf, in leaves of different age, and in different plants. It often reaches a thickness nearly twice the height of the glands, *i.e.*, about 76μ. (Pl. xxviii., fig.3).

In the older leaves, the glands lose their activity, the secretion becomes less mobile, and, in drying up, cracks along radiating lines. It is at this stage that the leaves present a lacquered appearance. The glands, being no longer functional, cease to grow, whilst the neighbouring epidermal cells enlarge considerably, and, as a result, the glands ultimately appear to be sunken (Text-fig.3). The dried secretion falls off when the leaf reaches its succulent condition, small patches, of negligible quantity, being restricted to the region of the glands.

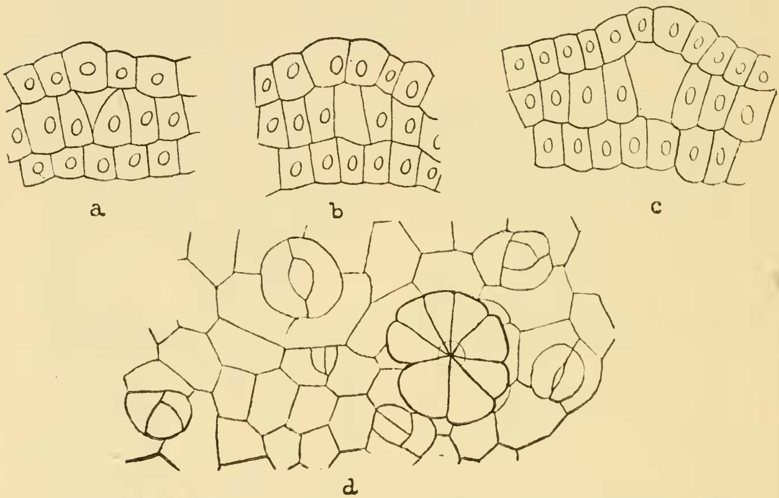


Text-fig.3.—Sunken, glandular hair in a mature leaf; ($\times$530).

The Development of the Stomata.

It is obvious that any stomata which are present on the young leaf coated with its sticky secretion, cannot be functional. In correlation with the rapid growth of the leaf-area, new stomata are continually being formed. Thus, in a section parallel to the surface of a young leaf, all stages in development of the stomata may be studied, as well as a small percentage of stomata which have already reached maturity (Text-fig.4).

Solereder (**4**, Vol. ii., pp.1079-1080), when classifying stomata, refers the Goodeniaceæ to two groups; (1) where there are no subsidiary cells, and (2) where subsidiary cells are formed parallel to the pore. In *S crassifolia* there are no subsidiary cells. A single epidermal cell divides by an oblique wall into two cells of unequal size. The larger of these cells remains an epidermal cell, while the smaller is the mother-cell of the guard-cells. The only further division which takes place is that which forms the two guard-cells. The mature stoma is surrounded by a variable number of epidermal cells (Text.fig.4*d*). The stomata reach



Text-fig.4.—Stages (*a-c*) in the development of the stomata, as seen in transverse section of young leaf: *a*, initial stage, showing mother-cell of the guard-cells; *b-c*, showing development of two guard-cells; no pore is formed; *d*, surface-view of young leaf, showing stages in development of stomata; (×300).

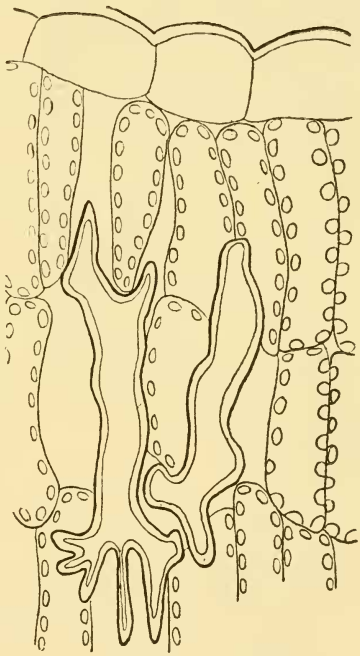
their full development when the flow of secretion has ceased. Those which mature first, are rendered functionless, for a time at least, owing to the blocking of their pores with resin. It seems highly probable that many of those stomata, in which a plug of resin is found enclosed in the stomatal aperture, will never function (Pl. xxviii., fig.4). Only those stomata which are belated in development, and are freed before reaching maturity, by the drying-up and cracking of the resin, are entirely unblocked by the secretion.

In those plants with lacquered leaves, which Volkens(**6**) described, such as species of *Brachylæna*, *Baccharis*, *Escallonia*, etc., the stomata are belated in development; and, in a few cases in which the secretion remains active until maturity of the leaf, the stomata become elevated until they project above the surface of the secretion. The mature stoma of *S. crassifolia* remains at the surface-level of the leaf. There is little of interest to remark in the structure of the mature stoma, a small, outer chamber being formed in the usual way, by an overhanging lip of cuticle.

Internal Development of the Leaf.

As in the case of the stomata, the development of the leaf-tissues is belated. In a young leaf just freed from the bud, there is no internal differentiation except that of the vascular system. The leaf, at this stage, is made up of a compact mass of rounded cells, the vascular strands occupying a median position. It is only when the secretion becomes less active, that differentiation of the leaf-tissues takes place.

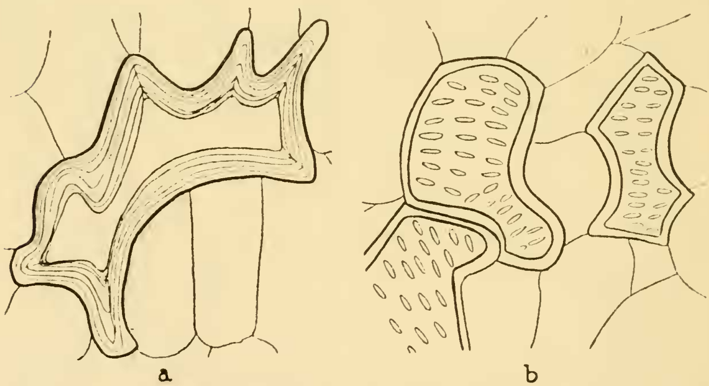
The fully-grown leaf of *S. crassifolia* is very thick and succulent, owing to the development of secondary, water-storage parenchyma. The epidermal cell-walls show a great development of cellulose, but are only moderately cuticularised. There is no spongy mesophyll, the greater part of the leaf being made up of several rows of palisade-cells. A tissue of rounded cells, amongst which are situated the vascular strands, occupies a median position in the leaf, and is bounded on either side by, sometimes, as



Text-fig.5.—Section of mature leaf showing occurrence of branched mucilage-cells in the palisade-tissue; (× 300).

many as five rows of palisade-cells. This central tissue is remarkable in the very old leaves, as its cells become enlarged, lose the greater part or all of their chlorophyll, and take on the function of water-storage. Those cells immediately surrounding the vascular strands are the first to assume the new function (Pl. xxviii., fig.5). From this central, water-storage tissue and from the palisade-tissue, special water-storage organs, such as mucilage-cells and water-storage tracheides are differentiated.

Mucilage-cells.—In the early stages of differentiation, certain cells, particularly in the palisade-region, develop mucilaginous walls. These cells keep pace with the growth in thickness of the leaf by branching in all directions, producing, thus, a peculiar and striking result (Text-fig.5). Text-fig.6*a* shows one of these branched mucilage-cells swollen after treatment with potash, and stained with corallin-soda to show successive deposits of mucilage in the cell-wall.



Text-fig.6: *a*, single mucilage-cell after treatment with potash, and stained with corallin-soda, to show stratification of mucilage; (×230): *b*, a group of water-storage tracheides from the central tissue of the mature leaf; (×400).

Water-storage tracheides.—Restricted to the central tissue are special water-storage tracheides occurring both at the bundle-ends, and in groups, quite independent of the bundles. They are of the type with thickened walls bearing transversely elongated pits (Text-fig. 6, *b*).

At the midrib, the tissues of the leaf merge into a compact chlorenchyma of rounded cells. The vascular strands are strengthened on both the upper and lower surface by a bundle of fibres.

Crystals of calcium oxalate are found in the cells of the leaf in very small quantity.

Conclusion.

The secretion of resin by glandular hairs in the bud and young leaves, and the lacquering of older leaves by the ultimate drying-up of this secretion, have been shown by Volkens (**6**) to be peculiar to some xerophytic plants. *Scævola crassifolia*, being a sand-dune plant, may be regarded as a xerophyte.

The chief ecological factors with which a dune-plant has to contend, have been summarised by Cowles (**2**, pp. 107-111). They are, (1), intense illumination, both direct and reflected; (2), the great divergence in the temperature-extremes, which is still further increased by the low specific heat of sand; (3), the drying action of the wind, and the injurious effects of wind-blown sand; (4), the porous nature of the sand, and its consequent low water-capacity. The third and fourth of these factors are, perhaps, the most potent. In South Australia, however, the first factor may have some considerable importance, since there are often periods of several days with cloudless sky, while the glare from the sun is still further intensified by the whiteness of the coastal sands.

As we have seen, *S. crassifolia* is able to survive burial in sand by an upward elongation of the shoot, and by the development of adventitious roots. By virtue of their thick, sticky secretion, the buds and young leaves are protected from desiccation, as are also the older leaves, owing to their succulence. A further protection from intense illumination is suggested by the yellow colouration of the secretion. The polished surface of older leaves, caused by the partially dried secretion, also serves to reflect certain rays of light.

The low water-capacity of the sand is compensated, to some extent, by the water-storage tissues of the older leaves.

Summary.

i. *Scævola crassifolia* is characterised by the development of peltate, glandular hairs, which secrete resin in great quantity. These hairs reach their maximum activity in the buds and young leaves.

ii. As the leaves become older, the glands become less active, the secretion loses its mobility, dries-up, and gives the surface of the leaf a lacquered appearance.

iii. The mature leaves of *S. crassifolia* are thick and succulent. The glands are sunken, and no longer functional on the blade of the leaf. They retain their activity only in the region of the leaf-base, protecting the axillary buds. Special xerophilous adaptations are found in :

(*a*). The secondary increase in size of the epidermal cells.

(*b*). The massive development of palisade-tissue.

(*c*). The development of special water-storage cells, such as mucilage-cells, water-storage tracheides, and ordinary, thin-walled, water-storage cells.

EXPLANATION OF PLATES XXVII.-XXVIII.

All figures were made at table-level, with the aid of Zeiss' camera lucida, with mirror at its greatest inclination, and with tube at 160 mm. Leitz objectives 3 and 6, and oculars 2 and 4 were used.

Plate xxvii.

Fig. 1.—A slightly oblique section through a bud, to show development of glandular hairs : *a*, stem-apex; *b*, rudimentary leaf; *c*, leaf-base; *d*, petiole of slightly older leaf; *e*, glandular hair; (× 160).

Fig. 2.—Section across sheathing base of a mature leaf, to show development of glandular and clothing hairs; (× 160).

Plate xxviii.

Fig. 3.—Part of section through young leaf, to show depth of secretion and outline of glandular hairs; (× 530).

Fig. 4,—Section of a lacquered leaf, to show patch of secretion blocking mature stoma; (× 300).

Fig. 5.—Section of a mature leaf : *p*, palisade-tissue; *c*, central water-storage tissue; *m*, mucilage-cell; *t*, water-storage tracheides; (× 100).

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